Patterns of population decline in birds

Real population declines . . . can be manifested in a variety of ways.

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INTRODUCTION

CONTINUING HABITAT LOSS and other forms of environmental deterioration impose even greater stresses on some of our most cherished bird species. While conservation is best achieved through proper habitat management, any type of interventionist approach is bound to produce mixed results, because no two species have precisely the same requirements. Thus, no matter how diligent our efforts to prevent the further degradation of our environment, some species are inevitably going to decline. It was the widespread recognition of this fact that led to the creation of the National Audubon Society's "Blue List" and that prompted the U.S. Fish and Wildlife Service to institute the annual Breeding Bird Survey. The objective of these efforts was to establish an early warning system that would pick up the danger signs of a population decline well ahead of the onset of an emergency.

While this objective is indeed a desirable one, the detection of legitimate as opposed to false danger signals is by no means a trivial task. The difficulty of distinguishing between significant population declines and normal year-to-year population fluctuations can be appreciated when one reads the conflicting regional accounts that often appear in the annual status reports on blue-listed species. There are really two difficulties here. One is the purely statistical challenge of distinguishing real trends from noise in census data. The other arises out of the fact that real population declines, at least in their early stages, can be manifested in a variety of ways. In this article we shall bypass the statistical issue (to be considered elsewhere) and focus on the types of changes in density, distribution and habitat use that can accompany general population declines. An examination of the patterns may serve two beneficial purposes. First, it might call attention to certain types of potentially serious declines that could go unnoticed or be dismissed as uninterpretable noise in the record. Second, by relating the patterns of decline to probable causes through analogy to well-documented case histories, one might, in the future, be able to draw inferences about where and how populations are being affected. We shall begin by considering how a general population decline may be quite differently manifested in breeding populations depending on the species' dispersal behavior.

RESIDENTS *VS.* MIGRANTS

SPECIES MAY BE roughly classified as either resident or migratory, although we recognize that many species contain both resident and migratory populations. The situation of resident species is relatively simple because most show strong philopatry; that is, individuals do not disperse far from their birthplaces. In such species, population declines can confidently be attributed to local causes, such as overhunting, habitat deterioration and pollution. The Wild Turkey (*Meleagris gallopavo*), Greater Prairie-Chicken (*Tympanuchus cupido*), and California Brown Pelican (*Pelecanus occidentalis californicus*) provide examples of declines attributable, respectively, to these three causes. The reader can no doubt add to the list. Because the causes of declines in resident populations are easily deduced in most cases, we shall not consider them further.

Migrants, especially long-distance migrants, deserve our special interest because habitat destruction is occurring at an unprecedented rate on the wintering grounds of many species (Terborgh 1980). Habitat loss in the tropics has not represented much of a threat historically because until recently habitat modification has been far more extensive in North America than it has in the countries to the south. If one assumes that the amounts of habitat available on breeding and wintering grounds were approximately in balance in pre-colonial times, then we can ask what the likely situation is today Eastern North America underwent widespread deforestation in the nineteenth century, with the resultant loss of perhaps half the original habitat available to forest-dwelling species. Deforestation in most New World tropical countries was much less extensive during the same period, so that by the beginning of the present century, wintering habitat for forest birds was presumably in excess. Since then, the amount of forest in eastern North America has stabilized or even increased somewhat, while deforestation in the tropics has been accelerating. Current estimates indicate that the amount of forest cover in Central America and the West Indies has been reduced by about 50%, so that the amounts of breeding and wintering habitat may again be roughly in balance (Myers 1980). All indications suggest, however, that the restored balance will only be transitory, and that the trend in the future will be one of decreasing availability of forested wintering habitat relative to breeding habitat. For birds wintering in fields, hedgerows and weedy pastures, the trend will obviously be in the opposite direction. Major shifts in the proportions of different kinds of wintering habitat available to migrant birds in the tropics can thus be expected to result in changes in the population densities, geographical ranges and habitat use of many species on their North American breeding grounds.

The interpretation of population trends in migratory species is complicated because adverse conditions can be encoun-

tered at any point in the migratory circuit (Morse 1980, Winstanley *et al* 1974) If one is to understand the implications of an observed change in abundance, it is very helpful to have some essential facts about the species' dispersal habits. In particular, one would like to know the average distance between an individual's birthplace and place of first breeding, and whether individuals that breed in a given region also winter in a coherent region. Although both these questions are highly relevant to the interpretation of population trends, for many migratory species neither question can be adequately answered. Nevertheless, different behaviors lead to distinct population responses, and so the questions must be faced even if the answers lie beyond our present knowledge.

If young birds return to breed near their birthplaces, then migratory species will react much like resident species to mortality or failed reproduction on the breeding grounds, *i.e.*, they will show strictly local responses to local perturbations. However, if dispersal distances are long, as they appear to be in several flycatchers (Whitcomb *et al.* 1981), then local effects could potentially be damped out by an influx of new birds each year. In this situation trends may be recognizable only if they involve large population units, *e g* , subspecies.

The pattern of migration to the wintering grounds is also important. A population that moves *en masse* to a discrete wintering ground is especially vulnerable to loss of winter habitat, and such habitat loss may translate directly to depressed densities on the breeding ground. An example of such a population is the Bicknell's Gray-cheeked Thrush (*Catharus minimus bicknelli*), which breeds in the mountains of New England and eastern Canada and winters in the West Indies and Venezuela, while the nominate subspecies (*C. m. minimus*) winters in northern South America from Colombia to Peru (A.O.U. Check-list 1957). Such discrete transposition of breeding populations onto wintering areas appears to be uncommon, however. Although far more data are needed, most breeding populations seem to scatter widely within the wintering range of the species. Consequently, the birds wintering in any particular area may represent two or more subspecies (Ramos and Warner 1980). In this case, a patchy loss of wintering habitat would have diffused effects on the breeding ground that might not be readily detected. A species that is experiencing reduced survival rates during migration or on the wintering ground may thus, depending on its dispersal behavior, show sharp declines in restricted portions of the breeding range, or changes of such a diffuse and gradual nature as to be below the threshold of detectability over the short run. Since the same cause (reduced overwinter survival) can produce different effects in different species, the task of recognizing danger signals is not at all easy.

LOCAL RESPONSE	GEOGRAPHICAL RESPONSE		
		retract from peripheral parts of a range	maintain full range
	maintain normal densities in all habitats	I	no population decline apparent
	retract from marginal habitats	II	IV
	reduced densities in marginal and optimal habitat	III	V

Fig. 1. The patterns of population decline. See text for details.

THE SIGNIFICANCE OF FLOATERS

NOW LET US SUPPOSE that a population decline has been unambiguously identified as lying outside the normal limits of fluctuation. The actual decline may be more severe than is suggested by measurement of breeding densities. Songbird populations may contain appreciable numbers of non-breeding individuals, commonly known as "floaters" (Stewart and Aldrich 1951, Hensley and Cope 1951; Morse 1971; Smith 1978; but see Brown 1969). These are individuals that are unsuccessful in competition for territories or mates; typically they are young birds that have never previously bred. The presence of floaters helps damp out fluctuations in breeding densities, because after winters of particularly poor survival, more of them will enter the breeding population than would normally. In the event of a general population decline, the first segment of the population to be eliminated will be the floaters, because competition for territories will be greatly diminished, and birds of low competitive status will succeed in entering the breeding population. In general, it is not known how large the floater population is in most species. If it is sizable, say 20 to 30 percent, then an equivalent population decline might be absorbed with little or no change in the observed density of occupied territories on the breeding grounds. Thus, a small observed decrease in the number of occupied territories may signal a much larger decrement in the population as a whole

Any event that reduces the overall population of a species without destroying its breeding habitat will permit a reassortment of breeding pairs. Such a reassortment can take several forms. Birds nesting in marginal habitats might move into vacancies in prime habitat. If so, the species would disappear from marginal habitats but maintain an unchanging density within prime habitat. Krebs (1971) demonstrated this response with experiments on Great Tits (*Parus major*) in England Optimal habitat for these birds is mixed woodland. Hedgerows are suboptimal, and birds nesting there have lower reproductive success. When Krebs removed territorial pairs from the woodland, they were quickly replaced by banded pairs from the nearby hedgerows. The vacated hedgerow territories were not refilled.

Another possibility is that a reduced population might continue to occupy the full range of habitats, but do so at reduced densities in all of them. Upon even further decline the species might vanish from marginal habitats and occur in sharply reduced densities in optimal habitat. Further stages of collapse may be signalled by the disappearance of a species from part of its geographical range The various patterns of reduced habitat use and range contraction that may accompany a general population decline are summarized in Figure 1. We shall now examine the case histories of some bird species that have undergone well-documented population declines to see what lessons can be drawn from hindsight.

CASE HISTORIES

Type I: Range contraction only

RANGE CONTRACTIONS UNACCOMPANIED by or unrelated to population changes elsewhere can occur in a number of situations: (1) extinction of a subspecies with a disjunct breeding range (Heath Hen, *Tympanuchus c. cupido,* on the Atlantic seaboard), (2) extensive persecution or habitat destruction in a portion of a species' range (Wild Turkey in New England and New York), (3) high mortality unrelated to habitat loss in a part of the breeding range (elimination of Carolina Wrens, *Thryothorus ludovicianus,* from parts of the northern periphery of their range in exceptionally harsh winters; see Wilds 1978). More commonly, range contractions occur in *conjunction* with widespread population changes, as a species disappears from peripheral regions of low population density. One example is Kirtland's Warbler (*Dendroica kirtlandii*).

Between 1961 and 1971, the known populations of this warbler declined by 60%, from about 1000 birds to about 400. The reduced population collapsed back toward the historical center of the species' range, leaving the peripheral areas virtually empty (Mayfield 1972a, 1973a, 1973b). Kirtland's Warbler is loosely colonial, and despite the decline, the density of birds in the remaining colonies was as high as in previous years. Mayfield attributed the decline to increased nest parasitism by Brown-headed Cowbirds (*Molothrus ater*). He did not believe the breeding or wintering habitat had changed appreciably over the course of the decade (Mayfield 1972a, 1972b). As virtually nothing is known of the biology of Kirtland's Warbler on its wintering grounds, however, the possibility of a loss of wintering habitat cannot be discounted (Terborgh 1974).

Type II: Range contraction and reduced densities in marginal habitat

We know of no cases to document this pattern, but it should not be dismissed as a possibility.

Type III: Range contraction and reduced densities in optimal and marginal habitat

Least Bell's Vireo (*Vireo bellii pusillus*): This geographically isolated subspecies once ranged from northern California south to 30°N latitude in Baja California. Between about 1930 and the present, it abandoned the northern portion of its range. Today, in California, it occurs in only seven counties, six of which are clustered in the extreme southern part of the state. Within these seven counties, the bird has vanished from areas it formerly occupied, even though the habitat appears suitable (Goldwasser *et al.* 1980; see also Fig. 2). The highest breeding densities in California today are far below values from the early part of the century. The causes of the decline are uncertain, but Goldwasser *et al.* (1980) suggest that habitat destruction and cowbird parasitism have played a role. A recent survey in Baja California (Wilbur 1980) found the birds missing from some historic locales, but present in relatively large numbers in others. These changes may be attributable to habitat modifications, but unfortunately, historical census data for the Mexican populations do not exist.

Type IV: Reduced densities in marginal habitats; no range contraction

Black-throated Green Warbler (*Dendroica virens*): Between 1969 and 1974, Morse (1976) studied the population dynamics of this species at several localities in Maine. These included a Red Spruce forest (Hog Island) and a White Spruce forest (Hockomock Point). Red Spruce is the preferred habitat, and the density of Black-throated Green Warblers was much greater on Hog Island than on Hockomock Point (74 pairs/40 ha *vs* 41 pairs/40 ha). Following two successive summers of unusual rain and fog (1972, 1973), populations in 1974 were much reduced. This decline, however, was not uniform in both locales. On Hog Island,

Fig. 2. Least Bell's Vireo in California. The dark line denotes the known historical range of this subspecies in California. Closed circles represent areas surveyed by Goldwasser et al. *(1980) where no Bell's Vireos were found. "X's" represent areas where Bell's Vireos were found From Goldwasser* et al. *(1980).*

the warblers declined by only about 3%, while on Hockomock Point they declined by about 58%. Naturally, such changes are reversible, and one could expect a return to prior density levels in both habitats The persistence of such a habitat-specific decline, however, could provide one of the most sensitive indications of an incipient general decline.

Type V: Reduced densities in optimal and marginal habitat; no range contraction

Bachman's Warbler (*Vermivora bachmanii*): Few birds have vanished as mysteriously as this warbler. Stevenson (1972) provides an excellent summary of its recent history. Bachman's Warbler declined throughout the first half of this century, and by 1950 it was extremely rare This decline was greatest between about 1910 and 1930, and was felt *throughout* the bird's range. In the past 30 years there have been only a handful of widely scattered sightings. Bachman's Warbler surely has vanished from any marginal habitats it once occupied, and is vanishingly rare in what is presumably the best available habitat. The International Council for Bird Preservation Red Data Book (King 1981) suggests that destruction of the breeding and/or wintering habitat was responsible for the decline. Terborgh (1974) notes that the wintering habitat of Bachman's Warbler—mature tropical forests in Cuba and the Isle of Pines—has been almost entirely destroyed for sugarcane production.

CONCLUSIONS

WE BELIEVE THESE PATTERNS of population declines are of more than historical interest. They indicate that the first signs of a decline may come at the periphery of a bird's range or in the center, in marginal habitat or in optimal habitat. Furthermore, the dispersal behavior and population structure of some species will tend to obscure population changes, making the detection of a decline that much more difficult. Given these possibilities it may be unrealistic, for example, to expect all of the regional compilers of the Blue List to agree on the status of a species Indeed, if our goal is early detection of a decline, it would be dangerous to list only birds for which there was unanimous agreement among the compilers. If individual observers monitor the local avifauna in a variety of habitats (to ensure that both marginal and optimal habitats are covered for many species), and if compilers are alert to regional trends, we stand a better chance of promptly detecting a bird in trouble. As conservationists our best policy must be a conservative one—to regard any chronic decline as a matter of considerable concern. To do otherwise is to gamble with the fates of our threatened birds.

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